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Can trackers count free-ranging wildlife as effectively and efficiently as conventional aerial survey and distance sampling? Implications for citizen science in the Kalahari, Botswana

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A B S T R A C T

Estimating wildlife abundance is central to conservation. We compared two widely practiced standards for counting animals - aerial strip surveys and ground line transects - with interpreted counts of animal tracks. At equal sampling intensity in semiarid savanna with good visibility all three methods produced similar population estimates and precision for six large herbivores. This comparison adds empirical support for the use of track count data to estimate population density rather than being restricted to ambiguous indices of relative abundance. Although expected to capture more species than aerial surveys, we found line transects limiting because encounter rates by direct sightings were relatively low; a minimum threshold 40 observations was achieved for only 1/3 of antelope species in 648.4 km of transect. By contrast, animal track counts returned exceedingly high encounter rates that allowed estimation of abundance for the entire large predator-prey community and mapping density-distributions more completely. Unlike aerial surveys conducted by Botswana's wildlife authority, the track survey provided opportunity to involve local people in the research process. The track survey cost 40% less than the aerial survey, and could be reduced a further 3-fold if trackers collected data autonomously without motor vehicles. Counting animals by their tracks is ultimately constrained to regions with appropriate substrates. However, in suitable environments like the Kalahari, we suggest that a citizen science driven by expert local trackers could ultimately replace conventional wildlife counts, generating knock-on benefits to conservation beyond improved data.

1. Introduction

Efficient methods of estimating wildlife numbers in-situ are of fundamental importance to modern conservation, yet a limited number of approaches dominate the toolkit available to practitioners. Furthermore, wildlife managers in developing countries are influenced by prevailing literature on field methods despite local conditions favoring alternative approaches. This paper poses the question: Can Kalahari trackers collect equivalent information as the aerial survey and ground line transects (distance sampling) routinely conducted by Botswana's wildlife authority, and can they do it as efficiently? We sought an answer by comparing simultaneous counts made by air, ground line transects and tracks, their achievable precision, and evaluate efficiency in terms of encounter rates and survey costs. The question and answer are important, in developing countries especially, where both conservation and poverty alleviation are fundamental policy agendas (Agrawal and Redford, 2006), local involvement in conservation has become imperative (Hulme and Murphree, 2001), and simple cost-effective means of biodiversity monitoring are sorely needed (Danielsen et al., 2005). A brief overview of the three methods

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provides context and relevance to our specific comparison.

For counting large-bodied animals throughout Africa, Australia and North America, strip transects using fixed-wing aircraft continue to be the standard go-to. Several reasons contribute to this including: a) aircraft are the most efficient means of sampling large areas randomly and systematically regardless of topography and surface conditions that might otherwise constrain ground surveys, b) analysis and interpretation of bounded strip transects does not require equivocal assumptions nor modelling - the math is “simple, elegant and absolutely solid” (Caughley and Sinclair, 1994, pg 198), and c) long-term datasets using standardized methods entrench their inertia and foster a reluctance to abandon them for alternatives (Pople et al., 1998). Extensive evaluations of aerial counts throughout the latter 20th century led to the conclusion that undercounting bias is often severe, is unavoidable, and difficult to measure (Caughley, 1974; Pollock and Kendall, 1987). But at least such bias is predictably in the conservative direction, and strict standardization to stabilize it allows counts to be interpreted relative to one another as trends (Caughley and Sinclair, 1994). Others disagree (e.g. Schlossberg et al., 2016; Jachmann, 2002). As wildlife managers are ultimately constrained by budgets, schedules and practicality, aerial surveys continue to be a primary, and often the only, data source available for wildlife population numbers and trends, especially over remote land masses.

The line transect method, or distance sampling, was developed to address the practical impossibility of counting all animals within bounded strips due to visibility biases. The essential theory identifies the probabilistic relationship of decreasing detectability as distance from observer to object increases. Detectability is measured from sighting distances and used to estimate a sightability curve, from which effective strip width is defined, thus compensating for animals unseen. The “theoretical excitement” (Caughley and Sinclair, 1994), provision of free user-friendly software with continuing refinements (Thomas et al., 2010) and elaborate guidance on the topic (Buckland et al., 2001) has supported widespread popularity of distance sampling among field practitioners. DISTANCE software has been downloaded by over 30,000 users in 110 countries (Thomas et al., 2010), and applied to animals, plants and other objects in terrestrial and marine environments around the globe. The accuracy of a distance estimate rests on proper selection of the sightability curve. Despite early warnings from the field about assumptions unlikely to hold for some species of mobile animals (Burnham et al., 1980), and other practitioners noting the difficulty of gaining a minimum number of observations with which to estimate robust detection functions (e.g. Duckworth, 1998; Jachmann, 2001), distance sampling is recommended as a best alternative to aerial strip counts for counting low densities of mammals in savanna environments (Ogutu et al., 2006; Waltert et al., 2008; Msoffe et al., 2010).

Scientists have long recognized the advantage animal tracks pose over direct sightings in detecting wildlife, but have struggled to make inferences on absolute abundance from track data. Instead, tracks are typically considered indices of *relative* abundance and criticized for the fluctuating, unknown and unmeasured detection probabilities that link the index to true abundance (e.g. Anderson, 2001; Hayward et al., 2015). There is a notable literature on estimating abundance via identification of individual footprints (e.g. Jachmann, 2001; Sharma et al., 2005; Li et al., 2018), an approach limited to few megaherbivores and carnivores with small populations. Another stream uses regression to calibrate track indices to true abundance (e.g. Stander, 1998; Bobek et al., 2014; Winterbach et al., 2016), although this approach presupposes several independent estimates of density. Advances in occupancy modelling have also opened up new possibilities to estimating absolute abundance from track data (Thorn et al., 2011). Interest in tracks has revolved mainly around carnivores given their propensity to avoid detection by other means, while much less attention has been devoted to other taxa. A general and parsimonious relationship linking track indices to population density long employed to enumerate ungulates in the snowy regions of Russia has appeared only rarely in the English language scientific literature (Stephens et al., 2006). The Formozov-Malyshev-Pereleshin (FMP) formula makes it possible to derive estimates of absolute animal numbers from their tracks without the necessity of individual recognition, prior calibration with known densities, or circuitous occupancy modelling. Simulations have verified the FMP an unbiased estimator of population density (Stephens et al., 2006; Keeping and Pelletier, 2014; Jousimo and Ovaskainen, 2016), but limited empirical validations have been either confounded by time and space (Keeping, 2014) or considered few species (Keeping and Pelletier, 2014).

In Botswana, as most jurisdictions, the need for reliable knowledge for conservation decision-making eclipses research capacity. Over the past 30 years, Botswana has implemented a remarkable, yet increasingly cost-prohibitive, countrywide aerial survey program. Surveys now occur with less frequency and focus on limited portions of the country, even as pressure on wildlife habitat is increasing. Recognizing limitations, wildlife managers have begun inconsistently conducting line transects on the ground as a compliment to aerial counts. It is unclear just how much this effort adds to the information already gained by the aerial survey. Botswana's challenges and opportunities are not unique. Pivotal resource decisions are frequently made with limited or inadequate data, or no data at all (Sutherland et al., 2004; Cook et al., 2009). Budget-constrained trade-offs are made between wildlife survey methods, and difficult allocation decisions are required. The relative value of data gained through different survey methods in relation to their cost-effectiveness informs these trade-offs. Considering 80% of Botswana's land surface is covered with sand and there is a latent force of erstwhile hunter-gatherers with legendary tracking skills, there seems a good opportunity to develop citizen science based wildlife monitoring, but this potential remains unexplored. An examination of how such an alternative measures up to status quo would be useful. We attempt that in this paper.

2. Materials and methods

2.1. Study area

We surveyed Kgalagadi District 2 (KD2), a Wildlife Management Area (WMA) occupying 6425 km^2 in southwestern Botswana bound by Kgalagadi Transfrontier Park (KTP) to the south, KD1 and KD12 WMAs to the west and east respectively, and KD3 communal grazing lands to the north (Fig. 1). Boundaries are unfenced and wildlife ranges freely throughout a larger contiguous landscape. This area is near the geographic center of the Mega Kalahari sand sea, one of the most extensive surface deposits of unconsolidated sand in the world (McKee, 1979). Climate is semiarid. Scattered trees, shrubs and grasses overlay the sand creating an open savanna (Fig. 2). Sayre et al. (2013) classify this as the “Kalahari Camel Thorn Woodland & Savanna” ecosystem.

2.2. Transects

Since 1986 Botswana's Department of Wildlife and National Parks (DWNP) standardized their aerial wildlife surveys countrywide. The transect grid bisects the country following systematically spaced parallel lines of longitude, stratified to vary in sampling intensity by region. In the Kalahari, transects are separated by approximately 10.2 km. Thirteen such lines bisect KD2, averaging 48.8 km in length and totaling 648.4 km. These run roughly perpendicular to the KTP boundary and areas of increasing disturbance towards the north of KD2 (see Fig. 1). Transects are therefore favorably oriented to minimize variance between them.

The same transects flown by aerial survey were sampled for the ground surveys. Surveys occurred within a 9-day period (Oct 25th – Nov 2nd, 2015) to limit error accumulation from animal movements. To minimize bias due to surveyor disturbance, the majority of same-transect surveys were separated by at least one day. Of 39 possible

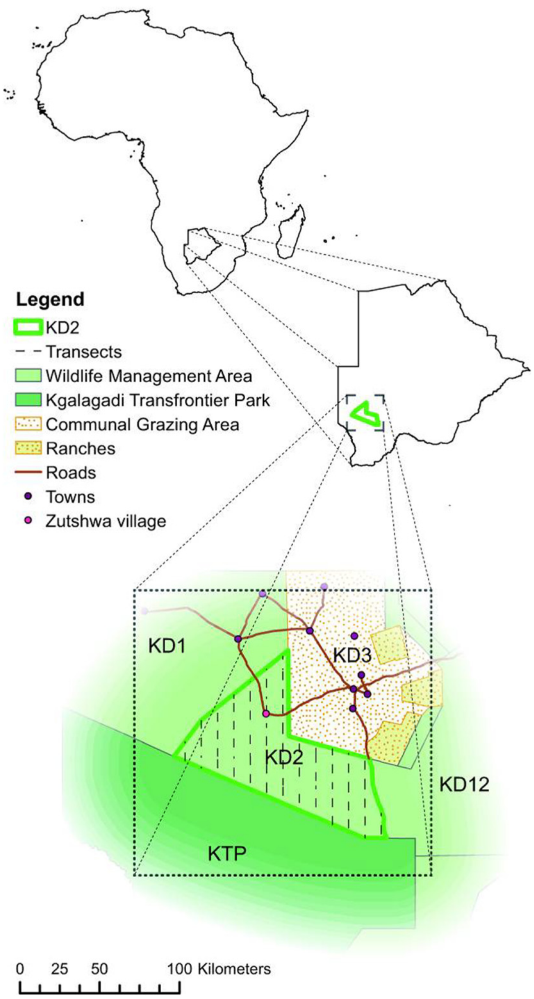

Fig. 1. Map showing the systematically-spaced transects sampled across 'KD2' Wildlife Management Area, and a geographic perspective of the KD2 study area.

temporally overlapping surveys, only 7 instances arose when two surveys occurred on the same transect during the same day; of those 7, there were only 3 exceptions when the aerial survey occurred simultaneously with a ground survey over short sections of transect. We do not expect these minor instances to cause any discernible bias between surveys.

2.3. Field surveys

2.3.1. Aerial counts

Aerial survey followed standardized DWNP procedures. Cessna 206 aircraft were fitted with navigational GPS and radar altimeter for height control at 91.5 m (300 ft). Aircraft were flown at 167 km h^{-1} (90 knots) while a data recorder seated in the front next to the pilot recorded sightings made by a pair of single observers seated behind in the next row. Multiple wildlife species were surveyed simultaneously including all antelopes and ostrich plus any other species incidentally observed. Markers attached to the lift struts delineated 150 m sampling strips calibrated for each observer looking out either side of the aircraft following Norton-Griffiths (1978). Altimeter readings were recorded consistently during the survey to calculate mean height above ground for each transect. Corrected total strip widths ranged between 299 and 347 m. Sampling intensity in KD2 was 3.64% by area.

2.3.2. Ground surveys

An essential aspect of both ground surveys was local expert observers. Most of the trackers involved in the field surveys reside in the remote village of Zutshwa. Trackers spent pre-1997 years hunting with subsistence game permits on their traditional territories in KD2, whereby tracking was a fundamental aspect of their livelihoods.

Ground transects were traversed with 4 × 4 passenger vehicles modified for long-range and equipped for remote survival. Data was collected by five teams, each with a driver, data recorder, and 2 trackers seated over the front of each vehicle. The trackers' positions afforded them a wide view of the ground and elevated eye levels compared to those seated inside the cab.

Ground crews endeavored to keep their travel path deviations within 30 m either side of the transect center line while navigating with GPS. Post-survey, we used ArcGIS to quantify spatial discrepancies by creating vertices every 11 m along the slightly meandering ground transects and measuring the nearest distances between those vertices and the flight paths.

2.3.2.1. Line transect distance sampling. We used conventional line transect distance sampling to collect direct sightings. Surveys commenced as early and continued as late as daylight permitted, although midday (11:00–16:00) was generally reserved for resting when heat and glare were intense. We surveyed at speeds 15–25 km h^{-1}. Animals were spotted by all passengers but most often by trackers. When sighted, observers stopped at the position where line of sight to the animal(s) formed a perpendicular angle with the transect and recorded object distance using a laser rangefinder. Species and group size where noted along with GPS location. When animals fled before observers reached the perpendicular position, range

Fig. 2. Semiarid savanna vegetation structure throughout KD2 study area showing typical visibility along a transect flown by aerial survey, and driven for distance sampling and track counts.

Fig. 3. View of sandy tracking substrate partially obscured by old and new grasses, with tracker pointing the way along a transect. Tyre marks are visible from the previous pass, outlining the sampling frame for track interceptions.

measurements were made to a shrub or tree marking their previous location. When animal(s) were observed by trackers only, they would walk to and interpret the place where the animal(s) was standing prior to disturbance so that an accurate distance measurement could be obtained.

2.3.2.2. Track counts. After completing line transects, the same teams conducted track surveys. For logistical ease, transects where tracked in the reverse direction back to each crew's first line transect starting point. Tyre tracks visible from the first pass outlined a consistent sampling frame whereby animal tracks that intruded the space between the tyres or on the tyre tracks were recorded (Fig. 3). In practice this relatively narrow space approximates a theoretical 1-dimensional transect because it is only a minute fraction (1 or 2 step lengths) of large mammal day ranges (Keeping, 2014).

Aerial surveys are limited mostly to large herbivores, so that was our focus. Although dwarf antelopes weighing < 20 kg such as steenbok (*Raphicerus campestris*) and duiker (*Sylvicapra grimmia*) are directly observed from the air and ground, for expediency trackers restricted their search image to large tracks, including large carnivores, so that the survey could proceed at speeds greater than the meticulous 6–8 km h^{-1} required to enumerate smaller species accurately (Keeping, 2014). Of the target larger wildlife species, trackers estimated the age of tracks, and only those created within the past 24 h were recorded. All track interceptions with the transect were counted and noted with GPS locations, regardless of whether trackers believed them to be the same individuals or not. Large herds were enumerated using handheld mechanical tally counters. Many of the trackers were illiterate. Irrespective of individual's linguistic or arithmetic ability, these simple devices removed distraction involved in mentally keeping a running count or verbalizing it, freeing the user's attention entirely onto tracks.

2.4. Theory - conceptualizing comparisons between direct sightings and indirect detections

Estimating the density of objects from indirect observations is not as intuitive as direct sightings. With direct sightings one strives to locate animals within space: sightings are made from a speeding aircraft before animals have time to flee outside of strip widths, or pinpointed from line transects before moving in response to observers. Density estimation follows rather straightforwardly, whether that be extrapolation of counts within fixed sample strips or applying sightability curves to estimate effective sample space.

Contrasting a "snapshot" model of animals as stationary objects pinpointed in two-dimensional space, indirect observations of tracks depend on the movement of animals to leave countable evidence of occurrence along what is theoretically a one-dimensional transect. The problem then is anchoring those animals to a two dimensional area. Borrowing from ideal gas theory in physics, the FMP formula is a random encounter model derived from the probabilistic intersection (track encounter) of lines of known length (transect and animal movement path) within an area. For a concise description of the main steps involved in its derivation, see Stephens et al. (2006). Thus, to estimate density one must obtain a measure of population day range of the species surveyed, corresponding to tracks made within that diel period of movement. The key assumption is random animal movements in relation to transects.

Fig. 4 illustrates relative areas over which objects are detected between transect methods. In this hypothetical example, aerial survey detected zero gemsbok, line transect detected one, and track survey detected 7 intersections by all 3 gemsbok. Clearly, most species exhibit daily movements that greatly exceed both aerial survey strip widths and the limits of view along line transects, resulting in higher encounter rates and a greater fraction of the study area effectively sampled by track survey. Differences in encounter rates are further magnified by the fact that a) individual animals can make multiple track interceptions, and b) animals that are within visible range during direct sightings can still be missed by observers. In contrast, without interference from weather the probability that day-old tracks are detected by Kalahari trackers approaches one. Notably, counting multiple track interceptions of the same individual animals does not introduce bias, but is actually necessary for obtaining an accurate density estimate (Keeping and Pelletier, 2014).

2.5. Population density estimation

For each of three methods, analyses of density were completed blindly by different co-authors.

Aerial survey data were analyzed with the program BASIS (Wint, 2007) using Jolly's method II (ratio method) for unequal-sized sample units (Jolly, 1969). The ratio method estimates density within the study area by extrapolating the ratio of animals counted to the area sampled.

Ground line transect data were analyzed with DISTANCE 6.2 Software Package (Thomas et al., 2010). DISTANCE software analyses data at the level of observation (individuals or groups of animals), those observations used to fit a detection function (sightability curve) to compensate for animals not observed. Buckland et al. (2001) recommended 60–80 observations as the minimum requirement for estimating robust detection functions, and an absolute minimum of 40. For species that did not reach this threshold, we pooled data from previous surveys in the region during 2002, 2004 (Wallgren et al., 2009) and 2007–2010 (DWNP, unpublished data) and settled for a minimum of 30 observations when necessary. Uniform, half-normal and hazard-rate key functions were fitted to the observed distances and their fit evaluated based on visual judgment and Akaike's Information Criteria. Data were truncated to improve fit, where appropriate discarding 5–15% of observations. Density estimates using the subset of observations from the KD2 survey were then based on these key fitted functions.

Track counts were converted to density by applying the FMP formula and non-parametric bootstrapping (Efron and Tibshirani, 1993) to estimate precision. The FMP model links track indices (track interceptions km^{-1} 24 h^{-1}) to true spatial density via the 24 h travel distances of the animals that made the tracks. We estimated species-specific day ranges allometrically and applied the correction factor for Kalahari species following methods outlined in Keeping (2014). Briefly, a database of day range (km) - body mass (kg) pairs for 22 species of Artiodactyla (Carbone et al., 2004) was resampled with replacement (n = 22), and a least-squares linear regression fitted to the $\log_e$ transformed data. We then predicted day ranges from this model applying the best estimate of average body mass for each Kalahari species. For

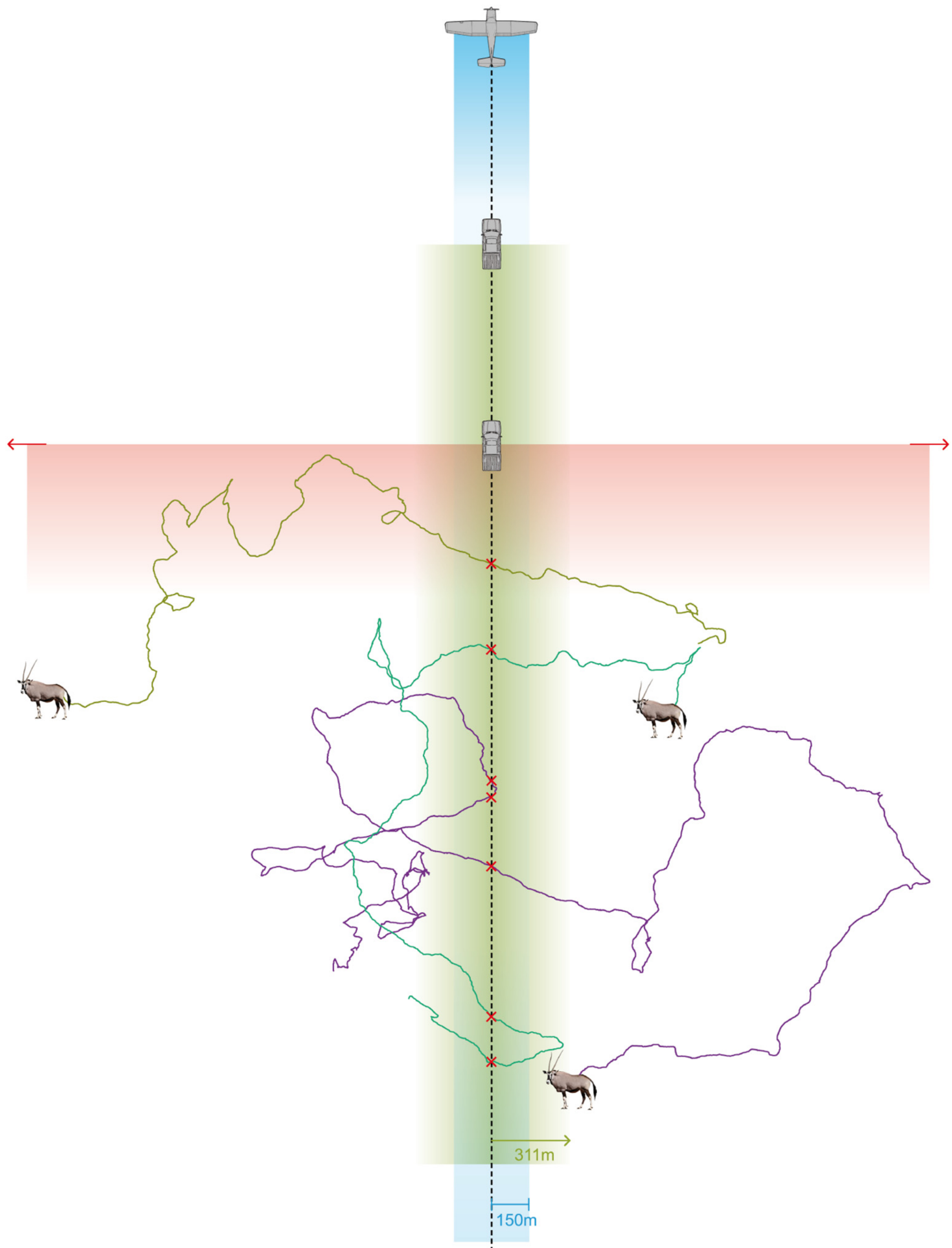

Fig. 4. Relative areas over which objects are detected by aerial survey (300 m strip width), followed by line transects (unbounded strip width, although in the present study 95% of observations occurred within 311 m from observers), followed by track survey (undefined strip, related to 24 h animal movements), in scale relation to three gemsbok (*Oryx gazella*) and their movements 24 h prior to surveying. Gemsbok movements were empirically traced by tracking from horseback (Keeping and Pelletier, 2014). Track interceptions are denoted by red x. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

track indices, transects were weighted by their length and resampled according to the proportional fraction that each transect comprised the total survey distance. The bootstrap mean track index was combined with day range into the FMP formula to create a single estimate of density. This process was repeated 5000 times to generate the dispersion of densities for each species, from which the mean and bias-corrected and accelerated 95% CIs were calculated. Exceptions were gemsbok (*Oryx gazella*) for which local empirical day range estimates were attained though trailing their daily movement paths (Keeping and Pelletier, 2014), wildebeest (*Connochaetes taurinus*) for which GPS collar data was available (M. Selebatso, unpublished data), and large carnivores whereby day range estimates were made through following habituated animals and GPS collars (Mills, 1990; Mills and Mills, 2017; Stander, 1998). A more sophisticated estimate of day range was attempted for cheetah (*Acinonyx jubatus*), outlined in Appendix A.

2.6. Encounter rates and survey costs

2.6.1. Encounter rates

For a comprehensive comparison of encounter rates we included all species for which prior data from the study region was available. We define encounter rate as expected number of objects detected per unit effort, the definition encompassing the mean distance (km) sampled per line transect observation (groups of any size), and per individual animal (for aerial survey and line transects), and per track interception. To calculate these statistics we pooled data from past surveys over a combined area including KTP and adjacent WMAs in both wet and dry seasons between years 2001–15. Spotlighting surveys provided line transect data for rare and nocturnal species (Wallgren et al., 2009). For species detected during both day and night surveys, we reported encounter rates for whichever sampling period that encounters were most numerous. Calculations were made from 42,614 km of aerial coverage;

11,242 km of ground line transects during the day and 2652 km of spotlighting at night; and 2233 km of track surveys for large herbivores and carnivores and 1602 km for remaining smaller species.

2.6.2. Survey costs

Inclusive in our cost estimates were the rental costs of the airplane and pilot, rental cost of suitable 4 × 4 vehicles, fuel, compensation for non-tracker personnel including trained aerial observers, drivers and data scribes, food and accommodation (where appropriate) and tracker compensation. While drivers and data scribes for the ground surveys were volunteers, we applied a low pay rate estimated from DWNP field officers as hypothetical non-volunteer personnel to make the comparison fairer. Excluded from the costing was standard non-consumable field equipment common to all surveys such as handheld GPS units. From the total costs of completing each survey of KD2 we calculated the cost km^{-1} sample effort. We then used these unit costs and the encounter rates to estimate the costs of accumulating species-specific observations.

2.7. Density-distribution maps

We generated species-specific maps in identical format to those routinely presented in Botswana's aerial survey reporting. These aerial survey maps have been the benchmark for inference about wildlife distributions in the Kalahari over the past 30 years (e.g. Verlinden, 1998), therefore, they are the standard to which alternative surveys can be compared. Resolution is dictated by transect spacing, ensuring that both transect length is maximized within each grid cell and coverage of the study region is complete. Thus, the study area was divided into grid cell squares averaging 112.4 km^2, each bisected through the center by a transect segment averaging 11.1 km. Observations along each segment were used to calculate point estimates of density within each grid cell. We quantified correspondence in density-distribution maps between methods using Pearson's correlation coefficients, suitable for zero-clustered data (Huson, 2007).

3. Results and discussion

3.1. Similarity among KD2 population estimates

Using 94,125 points of measurement between ground transects and flight paths, deviations between the two lines averaged 23 m (SD 31 m). As this is well within strip widths, we are confident that all three methods sampled the same populations on a per transect basis, and frequently the same individual animals.

The true number of wildlife in KD2 is unknown so the accuracy of estimates cannot be determined. Caughley and Sinclair (1994, pg 241) warned: “Most estimates of population size require that the manager makes a leap of faith. There is seldom any certainty that the population fits the assumptions of the model, nor whether the estimate is wildly inaccurate, nor whether the confidence limits have much to do with reality.” Nevertheless, undercounting bias is expected from aerial survey, and simultaneous ground counts are often employed to estimate that bias (e.g. Jachmann, 2002). As Distance sampling is widely regarded as more reliable than uncorrected strip counts, this provides a useful anchoring point for comparisons.

Raw counts of six large grazers were highly correlated among all methods (Tables 1 and 2). Slight reduction in population estimate correlation between tracks and direct sightings compared to raw counts (Table 2) hint that there was some error in the track-based density conversion, namely error in day range estimation. Despite this, no method appeared to return markedly different population estimates than another, and 95% confidence intervals showed large overlap between all three methods among large grazers (Fig. 5). Wilcoxon matched pairs tests showed non-significant results for contrasts between air-distance ($P = 0.92$), air-tracks ($P = 0.46$) and distance-tracks ($P = 0.46$), suggesting no systematic discrepancy in population estimation between the three different methods over the six grazers.

The similarity among estimates runs contrary to an extensive literature in which aerial surveys of conspicuous savanna ungulates typically return around 60% the numbers of ground counts (see summary in East, 1999 pg 91–92). In our surveys aerial estimates averaged 93% of line transect estimates, excluding wildebeest for which the aerial count was greater by a factor of 4. These results lend support to Botswana's multi-species counts of large grazers by fixed-wing aircraft in the southern Kalahari. Environmental specificity is an important caveat, and we add that our surveys were conducted during the late dry season before substantial leaf flush. Ground-truthing might reveal quite different discrepancies for the same species after leaf flush and in other areas of Botswana.

Contrasting grazers, a systematic pattern of undercounting bias from the air was apparent for browsers (Fig. 5). For kudu, duiker and steenbok, the aerial survey returned 60, 29 and 5% of line transect estimates respectively. Even greater disparity occurred between air and tracks, the aerial count returning 35% of the track-based kudu estimate. We suggest this is a true reflection of aerial undercounting bias because a) it is hinted in the raw counts: the air-track ratios for raw counts of large antelopes were neatly in the 1:10 range or higher with the exception of kudu for which that ratio was 1:25 (Table 1), and b) we trust the kudu track counts because their tracks are easily distinguished from similar-sized grazing antelopes even by non-expert observers. The diminutive steenbok appear most severely underestimated by aerial survey in the southern Kalahari. They are sand-colored, shade-loving, and usually do not move in response to aircraft. If counts typically return 5% of the true number of steenbok inhabiting this relatively open-country environment with good visibility, then undercounting discrepancies might be greater over the rest of the country.

Comparative density estimate percent Coefficients of Variation

Table 1
Raw observations by three survey methods along 13 transects (648.4 km) covering KD2 Wildlife Management Area.

	Air	Ground	Tracks
Species	Individuals counted	Individuals (observations) counted	Track sets counted
Eland	995	1774 (37)	9884
Gemsbok	584	333 (113)	4613
Hartebeest	133	250 (73)	1932
Ostrich	61	21 (12)	259
Springbok	104	131 (21)	1259
Wildebeest	170	111 (11)	735
Kudu	25	13 (6)	612
Duiker	12	12 (12)	–
Steenbok	48	267 (243)	–
Brown hyena	1	2 (2)	139
Cheetah	1	3 (2)	42
leopard	0	0	47
Lion	3	2 (1)	45
Spotted hyena	0	2 (2)	15
Wild dog	0	0	2
SUMS	2137	2921	19,584

Table 2
Cross-species correlations between methods for raw counts and population estimates for 6 large grazers.

	Aerial versus Distance	Distance versus Tracks	Aerial versus Tracks
	r (*P*)	r (*P*)	r (*P*)
Raw counts	0.916 (0.010)	0.960 (0.002)	0.982 (< 0.001)
Population estimates	0.965 (0.002)	0.790 (0.062)	0.831 (0.040)

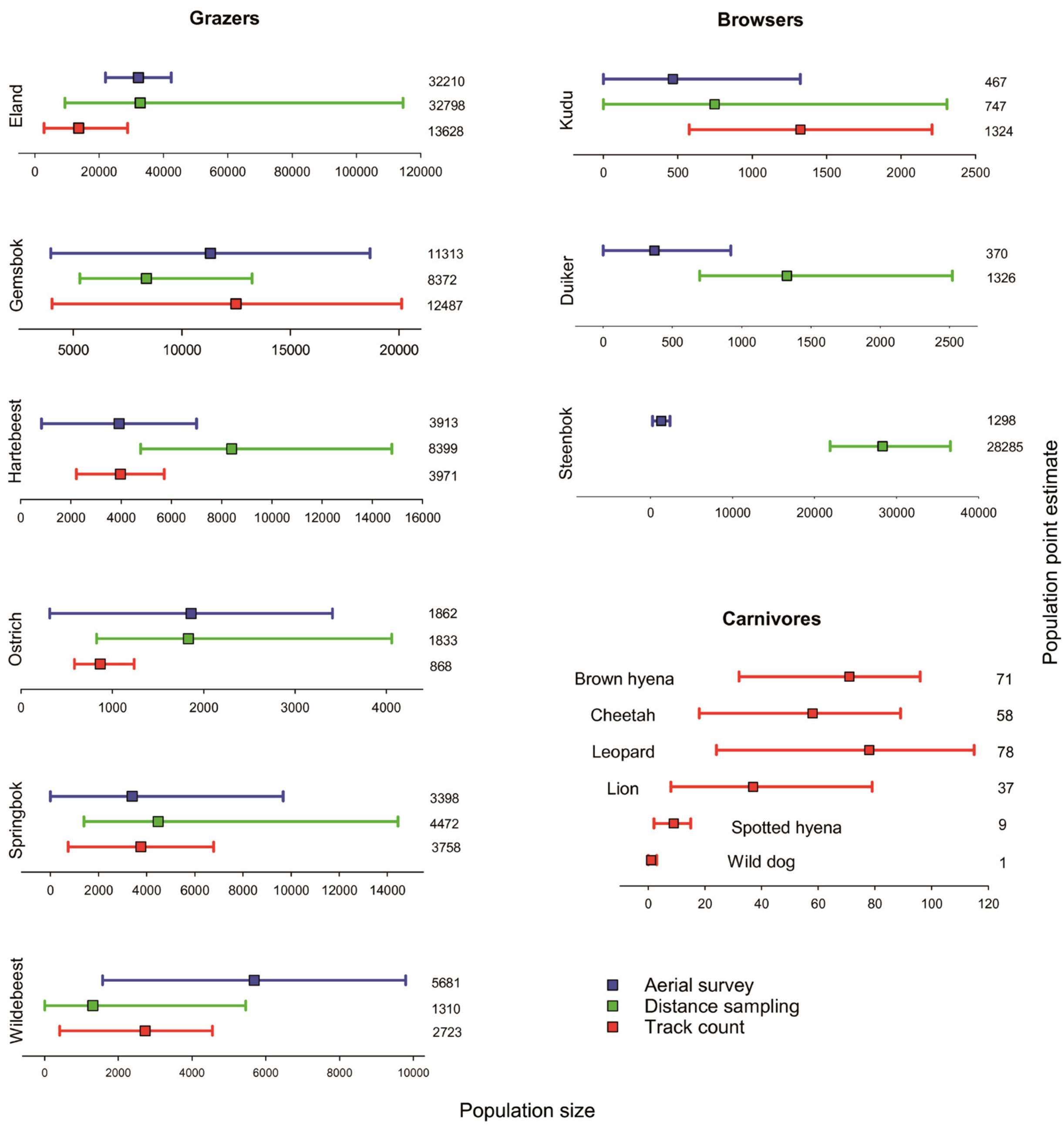

Fig. 5. Population estimates (number of animals) with 95% confidence intervals from aerial survey, distance sampling (ground line transects) and track survey in KD2 (6425 km^2). Note different x-axes scales for each species.

Table 3
Comparative density estimates, 95% confidence intervals and percent coefficients of variation between 3 survey methods for 9 antelope species in KD2 (6425 km^2).

	Aerial survey			Distance sampling			Track count		
Species	D	95% CI	CV(%)	D	(95% CI)	CV(%)	D	(95% CI)	CV(%)
Eland	5.01	3.41–6.60	14.7	5.10	1.46–17.83	68.5	2.12	0.44–4.49	55.0
Gemsbok	1.76	0.62–2.90	30.0	1.30	0.82–2.06	22.4	1.94	0.62–3.13	33.5
Hartebeest	0.61	0.13–1.09	36.4	1.31	0.74–2.30	28.3	0.62	0.34–0.89	25.2
Ostrich	0.29	0.05–0.53	38.4	0.29	0.13–0.63	41.3	0.14	0.09–0.19	27.4
Springbok	0.53	0–1.51	84.1	0.65	0.20–2.10	58.8	0.58	0.11–1.05	45.8
Wildebeest	0.88	0.24–1.51	33.4	0.20	0–0.85	74.9	0.24	0.07–0.41	39.9
Kudu	0.07	0–0.20	84.8	0.12	0–0.36	56.7	0.21	0.09–0.34	41.9
Duiker	0.06	0–0.15	68.9	0.21	0.11–0.39	30.8	–	–	–
Steenbok	0.20	0.04–0.36	37.4	4.40	3.41–5.69	12.1	–	–	–

(CVs) also showed close similarity between methods (Table 3), averages for 7 large antelopes being 46.0%, 50.1% and 38.4% for air, distance and tracks respectively. CV percentages exceeded thresholds of 20–15% typically considered suitable for monitoring trends, but this is unsurprising considering sampling intensity was a low 3–4% by air. In Kruger National Park, where game densities are higher, aerial survey CVs for most species of large grazers fell below the 20% target at relatively high sampling intensity (15%), while thereafter increasing intensity to 22 and 28% gave only marginal gains in precision (Kruger et al., 2008). Even at the highest sampling intensity some species, such as wildebeest, still failed to reach target precision. Encounter rate variance, a function of both variation in density among sampling units and sampling intensity, accounts entirely for the precision of aerial estimates, typically 70–80% of the precision in distance sampling (Fewster et al., 2009), and in this study roughly 72% of the precision in track-based estimates (the remaining 28% portion comprised of day range variance). Thus, with equal levels of transect sampling, more precise estimates of day ranges might marginally improve precision of track-based population estimates compared to direct sightings.

3.2. Survey efficiency - encounter rates and costs

Buckland et al. (2001) recommend collecting 60–80 line transect observations, and no < 40, to estimate reliable detection functions and resulting density estimates using DISTANCE software. By comparison, simulations have shown that FMP estimates experience small gains in accuracy and precision when sampling penetration exceeds 1 km/10 km^2 (Stephens et al., 2006; Keeping and Pelletier, 2014) - which was very close to that of the KD2 survey (648.4 km/6425 km^2). The KD2 surveys are therefore convenient for comparing which species can be profitably tackled by each method.

The difference between what is directly seen from an overhead or ground-level perspective, and what is detected by tracks after one diel period of animal movement in the Kalahari is remarkable (Fig. 6). Consistent for all species, track encounters accumulate over minute sample distances compared to direct sightings (Table 4). Similar discrepancies between line transect and track encounter rates have been noted before (Silveira et al., 2003; Fragoso et al., 2016). Despite open country with good visibility we had difficulty obtaining prerequisite minimum observations for common antelopes by ground line transects. Our study is not the first to comment on this shortcoming; the problem is pronounced in heavily forested environments (e.g. Barnes, 2001; Rovero and Marshall, 2004), but also tropical deciduous woodlands (e.g. Jathanna et al., 2003; Waltert et al., 2008) and more open savannas and grasslands (e.g. Harris, 1996; Ogutu et al., 2006; Nimmo et al., 2015). The recommended minimum 40 observations were achievable for only 1/3 of antelopes during the KD2 survey (see Table 1); the other species required supplements from previous surveys. We failed to assemble > 32 observations for duiker after pooling several survey efforts exceeding 11,000 km over a much greater area. Kudu detection rates were only slightly better. It would take roughly 12,000 km and 15,000 km of surveying to obtain 40 observations for kudu and duiker respectively (see Table 4). For this reason, with the exception of steenbok, ground line transects in the Kalahari add little to the aerial survey results.

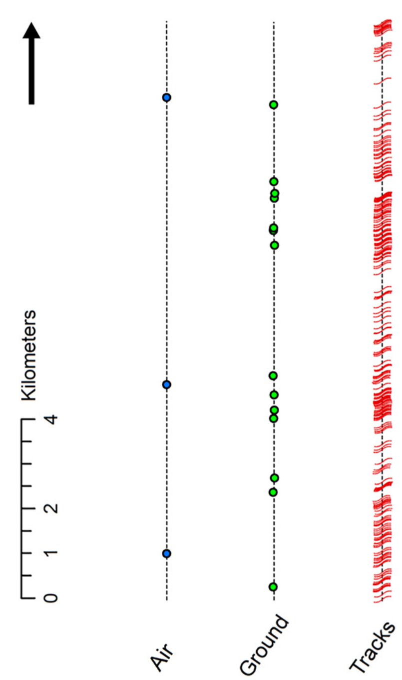

Fig. 6. Locations of encounters (combined antelope species) by aerial survey, ground line transects and tracks ($\leq 24\,h^{-1}$) along Transect 1 (12.7 km) in KD2.

In Table 4 we present 'inverse' encounter rates so that total sampling effort and cost can be quickly estimated for particular species when applying rules of thumb for recommended minimum observations. While it is often claimed that line transects are applicable to smaller, uncommon animals, a study of Table 4 shows that from an effort and cost perspective line transects are not practicable for many species in the Kalahari environment. For example, 442 km of spotlighting at a cost of $3171 USD is the expected sampling effort required to see an aardvark (*Orycteropus afer*). Attempting an aardvark density estimate by distance sampling with a minimum 40 observations would thus require 17,608 km of transect at a cost of $126,840 USD. By contrast, it takes an average of 3.9 km of surveying tracks for $28 USD to intercept an aardvark from the previous night. In the Kalahari the application of aerial strip counts is limited to large-bodied grazing ungulates. Unbounded line transects on the ground capture more smaller species, especially with night-lighting (Wallgren et al., 2009), but like aerial surveys the diversity of species that can be assessed with realistic levels of sampling effort is modest. Indirect, time-integrated observations of animal tracks overcomes the detection problem. Conservationists' interest in tracks revolves largely around carnivores because they elude detection by other means and are often conservation priorities. Our results suggest that track surveys have a more encompassing application than currently considered, whereby different groups of savanna mammals thought better counted by separate methods could be assessed simultaneously by tracks in the Kalahari at less cost than direct sightings methods. Extremely high encounter rates make it practical to assess the comprehensive mammalian community above threshold body size (Keeping, 2014).

3.3. Spatial density-distributions

Bearing in mind some animal movement between days that surveys occurred, overall there were remarkable correspondences in density-distribution patterns among different surveys, for all species (Fig. 7). There were moderate but mostly positive correlations between grid cell densities among methods (Table 5), although correlation strength was dampened by the fact that tracks had many more detections for which corresponding direct sighting grid cells had zero. Springbok, being both highly visible and having the most clumped dispersion of any species, showed the strongest correlations.

All species were consistently detected by their tracks in a greater number of grid cells than by direct observations (Fig. 7). The number of grid cells with detections were at least 50% greater in the case of gemsbok, but on average 3.3 times more grid cells by tracks than aerial survey, and 4 times more by tracks than line transects. At the most extreme, kudu were detected in 6.8 times more cells by tracks than by air and 8.5 times more cells by tracks than by line transect. These differences in presence detection are unsurprising as direct sightings are

Table 4
Comparative encounter rates and cost estimates (USD) per observation (groups of any size), individual animal and individual track set collected by aerial survey, ground line transects, and track survey for 35 species on conservation lands within Kgalagadi District, Botswana.

Latin binomial	Common name	Aerial survey		Line transect		Track survey	
		Km per (observation) and individual encountered	Cost per (observation) and individual encountered	Km per (observation) and individual encountered	Cost per (observation) and individual encountered	Km per individual track set $24\,h^{-1}$ encountered	Cost per individual track set $24\,h^{-1}$ encountered
Taurotragus oryx	Eland	(108) 9.3	$(1320) 114	(131) 4.5	$(940) 32	0.2	$1.43
Oryx gazella	Gemsbok	(12) 2.9	$(147) 35	(11) 2.2	$(79) 16	0.2	$1.43
Alcephalus buselaphus	Hartebeest	(35) 6.4	$(428) 78	(21) 3.7	$(151) 27	0.3	$2.15
Struthio camelus	Ostrich	(38) 17	$(465) 208	(33) 12	$(237) 86	1.6	$11
Antidorcus marsupialis	Springbok	(273) 19	$(3339) 232	(35) 2.3	$(251) 17	0.3	$2.15
Connochaetes taurinus	Wildebeest	(294) 27	$(3596) 330	(194) 39	$(1392) 280	1.4	$10
Tragelaphus strepsiceros	Kudu	(439) 132	$(5369) 1614	(304) 100	$(2181) 717	2.6	$19
Sylvicapra grimmia	Duiker	(168) 143	$(2055) 1749	(379) 331[a]	$(2719) 2375	1.6	$11
Raphicerus campestris	Steenbok	(22) 18	$(269) 220	(5.1) 4.1	$(37) 29	0.1	$0.72
Phacochoerus africanus	Warthog	(1291) 804	$(15,790) 9833	(1874) 1405	$(13,445) 10080	43	$309
Proteles cristatus	Aardwolf	?	?	(884) 884[a]	$(6342) 6342	6.1	$44
Parahyaena brunnea	Brown hyena	(14204) 14204	$(173,721) 173721	(221) 221[a]	$(1586) 1586	2.7	$19
Crocuta crocuta	Spotted hyena	(21307) 8523	$(260,594) 104240	(663) 126[a]	$(4757) 904	44	$316
Felis silvestris	African wild cat	?	?	(83) 74[a]	$(596) 531	2.9	$21
Felis nigripes	Black footed cat	?	?	?	?	55	$395
Caracal caracal	Caracal	?	?	(884) 884[a]	$(6342) 6342	7.9	$57
Acinonyx jubatus	Cheetah	(6088) 2507	$(74,459) 30662	(2248) 937	$(16,129) 6723	22	$158
Panthera pardus	Leopard	?	?	(331) 331[a]	$(2375) 2375	21	$151
Panthera leo	Lion	(2029) 1121	$(24,816) 13710	(884) 241[a]	$(6342) 1729	20	$143
Lycaon pictus	African wild dog	?	?	?	?	165	$1184
Otocyon megalotis	Bat-eared fox	(3874) 1639	$(47,381) 20046	(43) 21[a]	$(309) 151	0.4	$2.87
Canis mesomelas	Black-backed jackal	(384) 292	$(4969) 3571	(40) 35[a]	$(287) 251	0.3	$2.15
Vulpes chama	Cape fox	?	?	(58) 52[a]	$(416) 373	2.2	$16
Orycteropus afer	Aardvark	?	?	(442) 442[a]	$(3171) 3171	3.9	$28
Smutsia temminckii	Ground pangolin	?	?	?	?	93	$667
Xerus inauris	Ground squirrel	?	?	(67) 25	$(481) 179	5.0	$36
Lepus capensis &L. saxatilis	Cape & scrub hare	?	?	(38) 37[a]	$(273) 265	0.2	$1.43
Hystrix africaeaustralis	Porcupine	?	?	(295) 265[a]	$(2117) 1901	0.9	$6.46
Pedetes capensis	Springhare	?	?	(2.4) 1.6[a]	$(17) 11	0.3	$2.15
Mellivora capensis	Honey badger	?	?	(1249) 1124	$(8962) 8065	6.3	$45
Ictonyx striatus	Striped polecat	?	?	(2652) 2652[a]	$(19,027) 19027	2.0	$14
Galerella sanguinea	Slender mongoose	?	?	(336) 259	$(2411) 1858	55	$395
Genetta genetta	Small spotted genet	?	?	(115) 115[a]	$(825) 825	5.3	$38
Suricata suricatta	Suricate	?	?	(160) 21	$(1148) 151	12	$86
Cynictis penicillata	Yellow mongoose	?	?	(187) 146	$(1342) 1048	2.7	$19

?, no data.
[a] Line transect conducted at night by spotlighting.

Fig. 7. Population density-distribution maps over KD2's 6425 km^2 area for 7 large herbivores surveyed by aerial strip counts, ground distance sampling and tracks. Each map is labelled with percentage of cells occupied (N = 73).

constrained to relatively narrow strip widths and limits of view while tracks capture animals moving over larger areas (Fig. 4).

In the absence of other data over vast areas of the Kalahari, map outputs from Botswana's aerial survey such as those in Fig. 7 are increasingly relied upon to inform land use change discussions, namely relinquishing marginal portions of WMAs for livestock expansion. The contrasts in Fig. 7 show that vacant cells in Botswana's aerial survey maps are often false absences -an unsurprising artifact of low sampling intensity (3–4% by air). While counting animals is the primary objective, less equivocal distribution maps would be an additional benefit of

Table 5
Within-species correlations in density estimates between methods by map grid cell ($N = 73$).

	Aerial versus Distance	Distance versus Tracks	Aerial versus Tracks
Species	r (*P*)	r (*P*)	r (*P*)
Eland	0.728 (< 0.001)	0.190 (0.142)	0.211 (0.102)
Gemsbok	0.450 (< 0.001)	0.089 (0.494)	0.124 (0.339)
Hartebeest	0.624 (< 0.001)	0.360 (0.004)	0.401 (0.001)
Ostrich	−0.232 (0.072)	0.017 (0.899)	0.026 (0.844)
Springbok	0.998 (< 0.001)	0.934 (< 0.001)	0.934 (< 0.001)
Wildebeest	0.240 (0.062)	0.106 (0.416)	0.612 (< 0.001)
Kudu	−0.032 (0.804)	0.080 (0.540)	−0.062 (0.633)

implementing track-based surveys.

3.4. Implications for citizen science

Identifying nearly 20,000 tracks of similar-sized antelopes over few days is a remarkable feat. To our knowledge this is the first time a community in Botswana has not only participated in, but successfully led a wildlife count within their WMA. The distribution of remote communities in WMAs throughout western Botswana is favorable for implementing a rigorous citizen science at a large spatial scale comparable to its aerial survey. This citizen science presents several advantages over conventional methods (Box 1):

Firstly, resources severely constrain the capacity of Botswana's wildlife authority to survey all wildlife areas of the country at regular intervals. Whereas countrywide aerial surveys were being conducted annually in both wet and dry seasons during the 1990's, they now occur with up to three years intervening, in the dry season only, and are increasingly restricted to portions of the country. Similarly, ground line transects happen haphazardly. To survey KD2 by airplane cost \$7794 USD or \$12.02 km^{-1}, while the costs of both ground surveys were equivalent, each \$4652 or \$7.17 km^{-1} (Table 6). Despite substantial difference in time commitment required to survey KD2 (1.5 days by air; 15 team-days for each ground survey), the aerial survey was more expensive due to the aircraft, pilot, fuel, and accommodation for the crew. Thus, for equivalent levels of investment KD2 could be surveyed more frequently by ground than by air. Zutshwa trackers are also expert horsemen, and their horseback tracking skills have been utilized in previous research (Keeping and Pelletier, 2014). Horses remove the need for 4 × 4 vehicles which are by far the most expensive components of both ground surveys (Table 6). Similarly, CyberTracker software (Liebenberg et al., 2017) loaded onto inexpensive re-purposed smartphones remove the need for non-tracker field personnel time, as trackers can gather their own observations and upload data directly into a national database via cellular networks now present in remote communities. Assuming trackers on horseback would sample 25 km/day, or half the daily distance by vehicle and thus taking twice the number of team-days required to survey KD2, the total cost of a horseback track survey would be \$1400 USD - a threefold drop compared to using vehicles (Table 6). Camels offer further advantages over horses in terms of forage, water independence, and lion safety. Availability of funding and adequate resources are highlighted as the most likely limitations to implementing citizen science and community based monitoring (Chandler et al., 2017). Visitors accompanying Kalahari trackers on animal-back surveys is a creative possibility for funding citizen science, an option impracticable with conventional surveys conducted by wildlife authorities.

Table 6
Costs (USD) of surveying KD2 WMA (648.4 km of transect) by air, ground line transects, track survey using motor vehicles, and trackers without vehicles or supervision.

	Air	Distance	Tracks	Tracks (citizen science)
Survey team-days	1.5	15	15	30
Airplane and pilot	\$3371.73	–	–	–
4 × 4 vehicles	–	\$2400.00	\$2400.00	–
Fuel (avgas and diesel)	\$1293.28	\$236.85	\$236.85	–
Accommodation	\$1441.04	–	–	–
Subsistence allowance	\$246.94	\$823.12	\$823.12	\$823.12
Trackers	–	\$288.30	\$288.30	\$576.42
Personnel	\$1440.80	\$903.90	\$903.90	–
Survey cost	\$7793.79	\$4652.17	\$4652.17	\$1399.54
Cost km^{-1}	\$12.02	\$7.17	\$7.17	\$2.16

Secondly, trackers can simultaneously capture a broader picture of biodiversity. Our track survey generated population estimates for the six large carnivores inhabiting the region (Fig. 5), the majority of which are conservation priorities. At such low densities these species obviously cannot be surveyed by direct sightings and require an entirely different survey approach. Furthermore, if we had increased the track survey intensity, so halving the km coverage per day and doubling the total team-days to survey KD2, we could have captured the entire mammalian community at once down to small viverrids and lagomorphs (Keeping, 2014). Track-based detection may be the only practical means for monitoring rare and cryptic species over large areas of

Box 1
Key Advantages and Limitations of Citizen Science-based Track Survey compared to conventional Aerial Survey and Distance Sampling in the Kalahari.

Advantages:

- similar population estimates and achievable precision with equal transect effort
- higher encounter rates allow comprehensive species assessed simultaneously
- more complete spatial density-distribution maps, i.e. fewer false absences
- costs < 20% of the aerial survey if trackers use animal transportation instead of vehicles
- more frequent and comprehensive surveys = potentially more rapid/effective interventions
- participatory conservation, much needed employment

Limitations:

- reliable estimates of population day ranges at time of survey
- counting error accumulation with large herd sizes
- decline in traditional tracking skill levels (high consistency species identification, reliably aging tracks ≤ 24 h^{-1})

the Kalahari. Ground pangolin (*Smutsia temminckii*) is one example that is wholly data-deficient and an urgent global conservation priority (Heinrich et al., 2016) since pangolins have recently taken the unfortunate title as most illegally-trafficked wild mammals in the world (Challender et al., 2014). Tracker data addresses not only wildlife monitoring but also anti-poaching efforts.

Thirdly, long-term conservation will likely require community buy-in and participation. Since 2014 Botswana suspended hunting country-wide. This was motivated by publicised declines of certain antelope species in the Okavango Delta and vicinity (Chase and Landen, 2011; Gifford, 2013), the causes of which were ambiguous. As a blanket intervention the hunting moratorium is poorly resolved geographically especially as the aerial survey record shows stable or increasing trends in hunted species in the Kalahari over the last 3 decades, with the exception of springbok (DWNP, 2015). Enforcing the moratorium requires additional high costs of increased anti-poaching patrols against remote communities that were previously benefitting from subsistence and commercial wildlife utilization. These communities have long expressed dissatisfaction over their lack of involvement in wildlife counts, and skepticism of aerial survey results (Phuthego and Chanda, 2004). A step towards some local involvement in wildlife monitoring would likely catalyze knock-on effects beyond the volumes of new field data available to wildlife managers, that ultimately benefits conservation. Without tangible benefits from wildlife through utilization or involvement in local conservation human-wildlife conflicts predictably increase (Mbaiwa, 2018), and without livelihood alternatives poorly managed livestock expansion is the default direction in which land use tends to gravitate in the semiarid Kalahari.

3.5. Limitations of the track-based approach

Estimating animal numbers from their tracks requires knowledge about their day ranges. Error in day range estimation compared to the true movements of animals within the study area at the time of the survey, and extra-survey field effort required to reduce this error, are valid criticisms of the approach. We used allometry to approximate population day ranges for most large antelopes in the present study. Fortunately, the accuracy of population estimates relies overwhelmingly on the accuracy of track counts, and less on the accuracy of day range estimates. Although both are proportional to density in the FMP formula, that is a doubling or halving in either track numbers or day range equates to a doubling or halving of density, in reality animal densities typically vary over a much greater scale than do those species' respective day ranges. Among large herbivores in the present study, track counts varied over an order of magnitude (Table 1), while true day ranges are unlikely to differ by much greater than a factor of two. Field-estimating day ranges accurately is not greatly limiting in the Kalahari, where trackers can obtain fine ruler tracings of animal movements (i.e. 1 s GPS fix rates) by following animals' tracks (Keeping and Pelletier, 2014). Critics may argue that detectability is intrinsically measured in line transect observations and therefore distance sampling is a superior approach. The practitioner must decide if the excessive sampling efforts and costs required to obtain minimal observations with which to estimate detectability is a better allocation of resources than tracing a sample of animal movements to obtain empirical estimates of day range.

Inaccurate counting of large groups by their tracks is another concern. Eland (*Taurotragus oryx*) showed potential for underestimation (Fig. 5, Table 3). They were concentrated into large herds, some exceeding 1000 animals. When such sizeable groups intercept a transect, tracks laid down by animals at the front of the herd can be erased by hooves at the rear of the herd, making it impossible to count tracks accurately when masses are moving in long linear shapes especially. The challenge of enumerating large groups of animals by their tracks requires further investigation. To be fair, eland raw counts were strongly correlated with direct sightings, so it is possible that an inappropriate day range caused the discrepancy between population estimates. Also, counting bias of large herds is not exclusive to track surveys; it affects direct sightings substantially (Sharma et al., 2000; Frederick et al., 2003), and it is best practice during aerial surveys to photograph groups numbering 20 or more (Norton-Griffiths, 1978; Jachmann, 2002).

Finally, track surveys are limited by skilled observers, i.e. those who can correctly identify tracks to species with > 95% consistency, and reliably age tracks $\leq 24\,\mathrm{h}^{-1}$ old. Few tests of track identification skills among wildlife professionals have shown that even experienced field observers are often far below this high standard required for scientific monitoring programs (Evans et al., 2009; Zielinski and Schlexer, 2009; De Angelo et al., 2010). By contrast, Kalahari trackers have demonstrated near-perfect accuracy, even in identifying individual large carnivores and reconstructing their complex behaviours (Stander et al., 1997). But like spoken language and other aspects of indigenous cultures, tracker skills are in decline. In the Kalahari, the remaining pool of trackers with requisite skills is still large, but without a modern application to replace traditional hunting, talent will inevitably diminish with time.

4. Conclusion

We have helped Kalahari trackers demonstrate that their data rivals those collected routinely by wildlife authorities using conventional methods. Besides continuing standard surveys in the Kalahari for the purpose of consistency in long-term monitoring, we found little evidence that direct sightings are superior to tracks in terms of achievable precision, species comprehensiveness, distribution mapping, and costs. Rather, the track survey showed advantages in all these aspects. Given the exceptional opportunities presented in the Kalahari, we urge Botswana to consider track-based wildlife counts led by citizen scientists at a large scale to complement its aerial survey.

Across Africa and beyond aerial surveys will continue to be invaluable for counting large-bodied wildlife over huge areas, but bounded strip counts will not improve by great measure anymore. Similarly, distance sampling has become indispensable given the ability to measure detectability from sightings data and widespread applicability across taxa and environments, but ongoing refinements will bring only marginal gains. By contrast, track-based density estimation can benefit greatly from increased attention. Line transect development in the 1980's revealed a “rich lode of theoretical gold” that drew excitement and interest away from bounded strip counts, the mathematics of which had been “cracked 50 years previously” (Caughley and Sinclair, 1994 pg 204). This fad in wildlife science has since shifted towards its most recent phase: camera-trapping. The explosion of attention devoted to remotely triggered cameras reflects in part the limitations of direct sightings (Rowcliffe, 2017). Ironically, advancements in estimating population density from camera captures without the need for individual recognition were influenced by FMP theory (Rowcliffe et al., 2008), thus converging on the solution Russian biologists devised decades earlier for the estimation of density from animal tracks. As the detection process between cameras and tracks is similar, both benefit by cross-pollination of theoretical advancements. Camera-trapping obviously has great versatility and widespread applicability in many environments. Climate change is rendering long-term snow tracking programs in boreal regions less viable (Helle et al., 2016), some of which may be ultimately replaced by camera-trapping programs. Although cameras return lower encounter rates than track transects (e.g. Silveira et al., 2003; Lyra-Jorge et al., 2008; Pirie et al., 2016), their popularity extends even to the Kalahari (Van der Weyde et al., 2018). These trends tempt a belief that cameras could ultimately render tracking redundant for conservation monitoring.

More is sacrificed than just data if extraordinary field craft disappears and is replaced by high technology. Exceptional track interpretation skills represent an intangible cultural heritage. Tracking is largely forgotten by industrialized societies, including scientists, even though it may have been fundamental to the evolution of human intellectual abilities (Liebenberg, 2013). The most advanced tracking skills that have survived into modern times are often found in the most remote and marginalized communities (Liebenberg et al., 2017). Retrospectively, decline in traditional tracking skills is attributable to the failure of governments to recognize subsistence livelihoods as a valid human endeavor. However, evidence suggests that uplifting trackers through involvement in conservation could reverse the trend. Over a two-year project where Kalahari trackers conducted field surveys using CyberTracker, Liebenberg (2013) noted their tracking skills improved dramatically to the exceptional level observed ten to twenty years prior when they were hunting on a regular basis. Liebenberg et al. (2017) suggest that "Only by developing tracking into a modern profession, will tracking itself survive into the future."

It is remarkable that destitute trackers from forgotten quarters of the globe possess advanced observation skills that greatly surpass trained wildlife professionals. From a data accuracy perspective, the present field survey was impossible without them. Is tracking replacement with aircraft, laser rangefinders and camera-traps justified? Maybe not on lands where local people have tremendous value to add, are invested in long-term conservation and are without jobs to replace their subsistence livelihoods. As a signatory to the UNESCO *Convention for Safeguarding of the Intangible Cultural Heritage*, Botswana is obliged to address the rapid loss of tracking skills, just as it is equally committed to develop biodiversity monitoring and conservation measures as a signatory to the *Convention on Biological Diversity*. Facilitating a rigorous citizen science whereby biodiversity monitoring is conducted by Kalahari trackers would address both objectives.

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